RESEARCH ARTICLE

Predicting the effects of climate change on future freshwater fish diversity at global scale

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Abstract

The aim of the present study was to predict future changes in biodiversity attributes (richness, rarity, heterogeneity, evenness, functional diversity and taxonomic diversity) of freshwater fish species in river basins around the world, under different climate scenarios. To do this, we use a new methodological approach implemented within the ModestR software (NOO3D) which allows estimating simple species distribution predictions for future climatic scenarios. Data from 16,825 freshwater fish species were used, representing a total of 1,464,232 occurrence records. WorldClim 1.4 variables representing average climate variables for the 1960–1990 period, together with elevation measurements, were used as predictors in these distribution models, as well as in the selection of the most important variables that account for species distribution changes in two scenarios (Representative Concentration Pathways 4.5 and 6.0). The predictions produced suggest the extinction of almost half of current freshwater fish species in the coming decades, with a pronounced decline in tropical regions and a greater extinction likelihood for species with smaller body size and/or limited geographical ranges.

Introduction

Predicting the consequences of climate change on organisms' geographical distribution and, consequently, on their biodiversity, is a complex and monumental task, but one which is necessary (Warren et al. 2018). A simplistic, but common, approach to achieve this aim has been the creation of so-called Species Distribution Models (SDMs). SDMs relate a dataset of species occurrences with the environmental characteristics of the areas in which these occurrences are observed, so as to derive predictions for various climatic scenarios. SDMs, however, can also be used to derive projections for other types of global change such as land-use or human density, so they are not restricted to climate change. SDMs may thus be considered forecasting models, in which prediction reliability is highly dependent on the quality of the data employed and the strength of the relationship between global change and species distributions. Unfortunately, when the outputs of these correlational models are evaluated using occurrence data from a different period, whether it be for hindcasting or forecasting, the results obtained are often unsatisfactory (Kharouba et al. 2009; Rubidge et al. 2011; Rapacciuolo et al. 2012; Eskildsen et al. 2013; Ko et al. 2013; Watling et al. 2013). The inability to correctly forecast the future distribution of species under other climatic scenarios is likely not only due to our lack of species-specific knowledge of the effects of the explanatory variables, but also due to certain characteristics of the modelling procedures used. SDMs require the inclusion of non-climatic variable predictors, which also influence species distributions; and it should also be considered that the general lack of adequate survey effort precludes the use of reliable absence data. These two major shortcomings hinder the estimation of the 'true' causal influence of climatic variables (Lobo 2016).

Freshwater fish appear to be a group which is especially vulnerable to climatic changes (Markovic et al. 2017) and at high risk of extinction (Collen et al. 2014) under predicted changes in hydrological regimes and warming climate. Freshwater fish have already experienced important shifts and changes in their distributions in response to recent climatic changes (Comte and Grenouillet 2013), which have dramatically affected riverine fish assemblage composition (Conti et al. 2015). SDMs have often been used to estimate the effect of climate change on freshwater fish species. However, the majority of studies have mostly been focused on species that populate cold-water habitats in temperate North American and European regions (Hauer et al. 1997; Comte et al. 2013; Filipe et al. 2013; Edwards et al. 2016; Ruiz-Navarro et al. 2016; Radinger et al. 2017). Consequently, there is an extreme geographical bias in these studies and very limited information is available on the potential responses of freshwater fish species inhabiting the southern hemisphere or the tropics (see Pelayo-Villamil et al. 2018). There have been papers pub-

lished on research at country-wide or continental scales (Booth et al. 2011; Markovic et al. 2012; Comte and Olden 2017; Markovic et al. 2017; Jarić et al. 2019). However, to date, no study has attempted to estimate the potential effects of future climate changes on freshwater fish at a global scale. In this approach, we consider a fundamentally holistic approach to studying many species at a global scale, in order to better understand the possible effects of climate change, rather than relying on the single species studies that have dominated the field of freshwater species research to date (Gallo et al. 2017).

The present study is not characterised by the use of complex algorithms with unreliable absence data; instead, we make use of the unique empirical data frequently available (occurrence observations) to infer the environmental conditions under which particular species seem to be able to maintain sustainable populations. This information was subsequently used to transfer spatial data on these suitable environmental conditions to potential future climatic scenarios. The purpose of this study, therefore, is to map the future location of the climatic conditions under which freshwater fish species are currently observed, assuming the general incapacity of freshwater fish species to colonise new river basins (Drakou et al. 2009) and obviating the role played by micro-evolutionary processes and phenotypic plasticity. Thus, the main aim of this study was to provide a general assessment of the most likely changes in freshwater fish species richness, diversity and body size in world watersheds, as well as to estimate the most plausible modifications in the distributional area of these species.

Material and methods

Occurrence records of freshwater fish

The dataset of geographical records for freshwater fish, developed by Pelayo-Villamil et al. (2015), was updated to reflect the taxonomic changes and new species described up to the end of October 2018. Appendix 1 in Suppl. material 1 describes all sources obtained from the Global Biodiversity Information Facility (GBIF; see https://www.gbif.org/), which were used in this study, in detail. Other sources, such as web pages, museum collections and published manuscripts are described by Pelayo-Villamil et al. (2015). Records were downloaded and filtered using the data cleaning capabilities available in the ModestR software (Pelayo-Villamil et al. 2012; García-Roselló et al. 2013, 2014, 2015). GBIF records were filtered as follows: i) records with the same latitude and longitude were excluded, ii) records with 0° latitude or longitude were also excluded and iii) habitat data were cleaned, in order to eliminate occurrences in habitats other than those corresponding to terrestrial freshwater ecosystems (see García-Roselló et al. 2014 for details). At the end of October 2018, 16,825 species of freshwater fish were recognised as valid by taxonomists and are available at IPez (http://www.ipez.es, Guisande et al. 2010). Of these, 16,662 species (99.6% of the total) had associated geographical information, for a total of 1,464,232 occurrence records (unduplicated). See Suppl. material 2: Table S1 for a detailed description of the

species included in the analysis, as well as future species predictions in 2050 and 2070 under both scenarios and the maximum body length of each species, all of which were obtained from https://www.fishbase.org/ or from the original manuscripts, when not available at FishBase.

Biological species traits to measure functional diversity

We used the classification described by Buisson et al. (2013), slightly modified, for functional description of the fish species. We used six traits divided into three biological functions: food acquisition, life habitat and locomotion. Food acquisition traits include the feeding habitat (pelagic, benthopelagic and benthic) and the trophic guild (primary consumer, secondary consumer, top-predator, omnivorous and detritivorous). Life habitat traits comprise habitat type (pelagic, benthopelagic and demersal) and migration type (potamodromous, anadromous, catadromous, amphidromous, oceanodromous and no migration). Finally, locomotion traits include body length (in cm: small < 15, medium 15–50, large 50–150 and extra-large > 150) and rheophily (rheophilic, limnophilic and eurytopic). The biological traits assigned to each species are available in Appendix 2 of Suppl. material 3. This information was obtained from https://www.fishbase.org/ or from the original manuscripts, when not available at FishBase (Froese and Pauly 2019).

It was not possible to include reproduction traits, such as life span, parental care or reproduction habitat, because of the difficulties inherent in the assignment of these functional traits to over 16,000 species.

Predicting future species distributions

The future distribution of species was estimated by a modelling procedure (NOO3D) available in the ModestR software (Pérez-Costas et al. 2019), which is based on a simple method called Niche of Occurrence (NOO; García-Roselló et al. 2013, 2014, 2019). NOO3D can be used both to estimate the 3D distribution of species using 3D occurrence samples and 3D environmental datasets (e.g. at different depths) and to extrapolate the probable distribution of a species at different time slices taking into account the occurrences available in one or more time periods. A full description of this procedure is provided in Suppl. material 4 (Appendix 3) and there is a step-by-step tutorial freely available at http://www.ipez.es/modestr/Manual_Tutorial.html (see also García-Roselló et al. 2019 and Pérez-Costas et al. 2019).

In essence, both NOO and NOO3D aim to overcome the drawbacks associated with the general lack of reliable absence information (Lobo et al. 2018), as well as the frequent use of arbitrary geographical extents (Acevedo et al. 2017). The procedure firstly delimits the Extent of Occurrence or the accessible area for each species using a convex hull, an α-shape or a Kernel density distribution. In this study, three separate delimitation methods were used to determine the accessible area, which included different α values, in the case of α-shapes and several smoothing values, in the case of Kernel

densities. Subsequently, the 19 bioclimatic variables of the WorldClim 1.4 database representing average climate data for the 1960–1990 period (www.worldclim.org; Hijmans et al. 2005) were used in ModestR to estimate the environmental values of the occurrence records. Future bioclimatic data of the RCP 4.5 and RCP 6.0 Representative Concentration Pathways (RCPs) coming from the same source were also used. We did not include other important variables in our analysis, such as catchment area, connectivity with other catchments, intensity of human activities etc., due to the worldwide scale of this study and the well-known relevance of climate variables in explaining large-scale species distributions (Pearson and Dawson 2003). From the available bioclimatic variables, only those that best explained the distribution of freshwater fish species were used (Manjarrés-Hernández et al. 2018); those with a Variance Inflation Factor (VIF) of less than 20 were selected. The VIF quantified the multicollinearity of predictors (Guisande et al. 2011) and, in this case, the VIF value was selected by deleting those variables which displayed the most severe multicollinearity because we are only interested in estimating the explanatory capacity of each predictor. Consequently, the following 10 bioclimatic variables were finally selected: annual mean temperature (BIO1), mean diurnal range (BIO2), isothermality (BIO3), temperature seasonality (BIO4), mean temperature of the wettest quarter (BIO8), annual precipitation (BIO12), precipitation of the driest month (BIO14), precipitation seasonality (BIO15), precipitation during the warmest quarter (BIO18) and precipitation during the coldest quarter (BIO19). Elevation was also included as a predictor because it seems to be a temporary, invariable, but important factor affecting the distribution of freshwater fish (Manjarrés-Hernández et al. 2018). Appendix 3 in Suppl. material 4 details the procedure followed to include the WorldClim 1.4 database as a 3D set of variables in the ModestR software. All these variables were handled at a resolution of $5' \times 5'$.

Subsequently, the relevance of these environmental variables to explain the distribution of each one of the species was estimated by using the Instability Index described by Guisande et al. (2017a) and Guisande (2018b) that does not require normalised data. Dividing each predictor into a number of intervals or bins determined by the user, the number of records in each bin was calculated considering separately the cells where the species occurs and those of the selected studied area. A peak of instability is observed when there are important differences in the predictor comparing the bins of presence with the corresponding ones of the study area. This index outperforms other methods proposed to identify the most appropriate environmental factors (Guisande et al. 2017a; Fan et al. 2018). The explanatory variables with the highest percentage contributions to the Instability Index would be those that most affect the distribution of the species in the accessible area. In order to include only those variables with a higher contribution, it is possible to select an accumulated percentage of contribution (the default option is 80%) so that, if 100% is selected, all variables will be included. It is important to highlight the fact that the software identifies the most important variables for each species and that these variables may vary between species.

Once the most important environmental variables which affect the distribution of each species in their accessible area were identified, all cells with environmental

conditions similar to those existing in the occurrence localities were delimited, thus predicting the changes in species diversity in the years 2050 and 2070, under the RCP 4.5 and RCP 6.0 climate scenarios. The most appropriate model outputs to be applied in NOO3D were selected by comparing estimated river basin species richness with the results of accumulation curves derived from occurrence records (Lobo et al. 2018). This entire process was automatically implemented in ModestR (see Suppl. Material 4).

Pelayo-Villamil et al. (2018) demonstrated that over 71% of countries worldwide have inventories of freshwater fish species that may be categorised as of poor quality. Furthermore, even those countries with relatively accurate reliable national inventories possess high degrees of variability in the completeness of their provincial or regional inventories. Therefore, species richness in river basins is doubtlessly underestimated when the raw geographical occurrence data are used. Species richness of freshwater fish in each river basin, then, was approximated with the *RWizard* (Guisande et al. 2014) application, *KnowBR* (Lobo et al. 2018; www.ipez.es/RWizard), also available as an R package on CRAN (Guisande and Lobo 2018). This application enables the use of information, which originates from exhaustive database records, to build species accumulation curves that describe the relationship between the accumulated number of species and a surrogate survey effort for different spatial units (such as cells, countries or river basins, as is the case here) simultaneously. These accumulation curves are adjusted to different asymptotic or quasi-asymptotic functions, in order to estimate the predicted number of species when the survey effort tends toward the infinite (Clench 1979; Soberón and Llorente 1993; Hortal and Lobo 2005). The default exact estimator was utilised to derive the accumulation curve and the Clench function applied for curve adjustment in order to estimate the potential number of species when the number of records tends toward the infinite. Occurrence records in level-two river basins (González-Vilas et al. 2016), which are available in ModestR (García-Roselló et al. 2013), were used as target spatial units. The species richness estimations obtained from *KnowBR* were considered to be the most probable species richness values present in the river basins and were subsequently compared to the species richness figures obtained after overlaying the outputs of the individual species models created by the aforementioned modelling procedure.

The final consequence of all this process is a geographic representation of each species' distribution area both for present and future scenarios, taking into account the climatic conditions of the observed occurrences. In this manner, the most probable future distribution of each species was estimated according to the information derived from current occurrences and in accordance with the values of the environmental variables in potential future scenarios (see García-Roselló et al. 2019). For those species with few records, for which it was not possible to estimate the probable distribution following the formerly mentioned procedure, the ModestR software was used to verify whether the current environmental conditions where the species is present will be available under future scenarios. In the case that the current environmental conditions in which the species are present were unavailable under future scenarios, the species was considered to be locally extirpated. We must emphasise that the performance of NOO3D relies on two fundamental assumptions: i) that current geographical occurrences can

infer suitable environmental conditions for each species, at least partially and ii) that these environmental conditions are the main drivers of species distribution or act as surrogates for the true causal variables. Presence is very frequently the only available empirical evidence that provides an image of the environmental conditions in which each species is able to maintain sustainable populations. Hence, transfer to other temporal scenarios in the climatic or environmental ranges obtained from observed occurrences must be considered provisional map representations, which are highly dependent on their capacity to colonise distant, but suitable, localities. Therefore, our study strives to describe the future location of areas which are accessible to the considered species and which will have climatic conditions similar to those in which the species is observed in the present day (Lobo 2016), while excluding the role played by microevolutionary adaptations.

River basins as spatial units for the estimation of diversity

The geospatial data for river basins imported into ModestR was obtained from the WaterBase project website (http://www.waterbase.org). WaterBase global river basin data were taken from the drainage basin dataset distributed with HYDRO1k, a hydrological database developed by the EROS Data Center of the U.S. Geological Survey (USGS). This database provides a collection of global geo-referenced layers at a 1 km resolution derived from GTOPO30, a 30 arc-second digital elevation model (DEM) of the world. The drainage basins dataset from HYDRO1k was projected on to latitude/longitude geographical coordinates. Vertices were smoothed by applying a 500 m threshold in order to generate the ESRI Shape files available via the WaterBase website.

The river basins dataset was originally obtained by combining flow accumulation and flow direction layers, which were, in turn, derived from the hydrologically-corrected DEM, based on the GTOPO30 dataset. The basins were organised according to the procedure first proposed by Pfafstetter (1989) and later adapted for use in the HYDRO1k dataset (Verdin and Greenlee 1998). River basins were divided into six levels and each sub-basin was identified using a unique Pfafstetter code, (i.e. a six-digit code with information about the interconnections of the basins).

We used level-two of the river basins data set (González-Vilas et al. 2016) as the spatial unit for the estimation of the diversity, because this level is the geographical extent that best illustrates the effect of environmental parameters on the distribution of freshwater fish species (Manjarrés-Hernández et al. 2018).

Diversity indices and statistical analysis

For each river basin, both in present and in future projections (2050 and 2070), according to the results obtained for the RCP 4.5 and RCP 6.0 scenarios, several diversity indices were estimated. The DER function from the R package *EcoIndR* (Guisande et al. 2017b; Guisande 2018a) is used for this purpose, which allows the calculation of 31 different indices for each river basin belonging to five categories: rarity (two indices),

heterogeneity (14 indices), evenness (seven indices), taxonomic diversity (two indices) and functional diversity (six indices; see table 1 in Guisande et al. 2017b). Since there is no index universally applicable to all ecological assemblages (Magurran 2004), the DER algorithm was also employed for the selection of the diversity indices that best showed the differences between river basins. Therefore, from all of the estimated indices, only one of each of category was chosen.

All statistical analyses were run with the *RWizard* application *StatR* (Guisande et al. 2014). Stepwise multiple regressions were performed with the stats R package (R Development Core Team 2018). A backward-forward approach, based on Akaike Information Criterion (AIC), was used to select the most parsimonious model. The relative contribution of each variable in the regressions was estimated with the LMG method (the r^2 contribution averaged over orderings amongst regressors) with the R *relaimpo* package (Grömping 2006, 2018). The *dwtest* function from the *lmtest* package was utilised (Hothorn et al. 2018) to estimate autocorrelation with the Durbin-Watson statistic (Durbin and Watson 1951).

Results

As expected, the regression slope between river basin species richness, estimated with accumulation curves and observed species richness, obtained from records (Fig. 1, red line) is significantly lower than one (ANCOVA, P < 0.001), with a value of 0.81. This means that river basin species richness is underestimated when using the available raw data and that the under-prediction is greater when basin species richness is high. This is likely due to the poor quality of existing inventories in many countries, especially in tropical areas which host a higher number of species (Pelayo-Villamil et al. 2018).

Amongst all of the procedures used to select the accessible area in the modelling procedures (convex hull, alpha shape with different α values, Kernel density with different smoothing values etc.), the model displaying the best fit when compared with the species richness estimated from accumulation curves was generated with a Kernel density estimator using a smoothing value of two. The intercept of this relationship was not significantly different from zero (ANCOVA, P = 0.292) and the slope was not significantly different from one (ANCOVA, P = 0.512) with a value of 0.99 (Fig. 1, blue line). As a result, the species richness data predicted with the kernel density estimator were selected to be imported into the temporal transfer modelling procedure, because the species richness was quite similar to that obtained from the accumulation curves.

The decline in species richness was very similar between scenarios RCP 4.5 and RCP 6.0. These models predicted the complete disappearance of the distributional areas of half of all freshwater fish species (from 45.3% to 46.7%, independent of the year or the climatic scenario). As an example of the predicted decline, Fig. 2 shows the predicted change in species richness in the year 2070, under the RCP 4.5 scenario. This decline was more pronounced in tropical river basins and was particularly high in Vietnam and south-eastern China (Fig. 2).
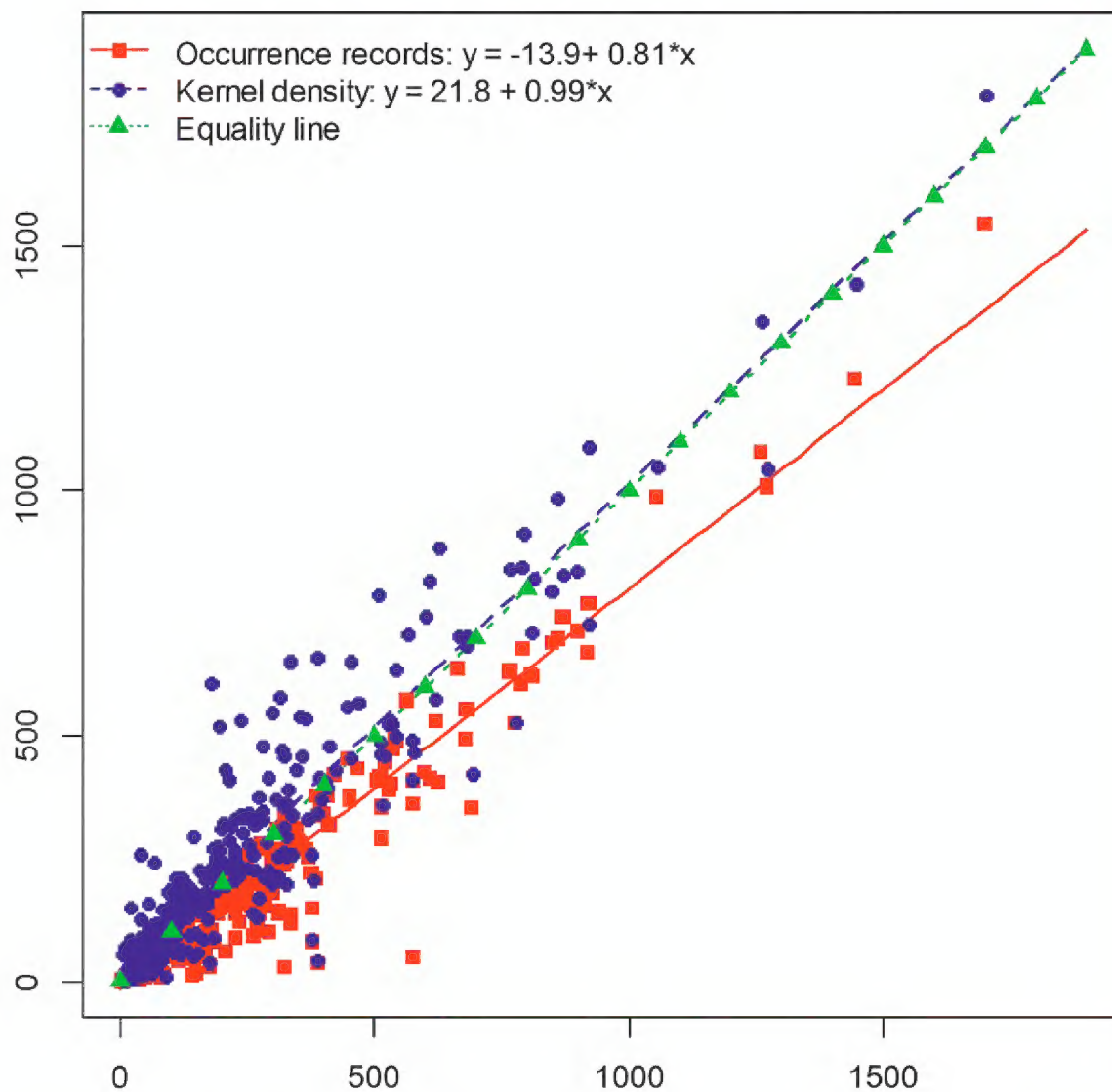
Figure 1. Relationships between the species richness in level-two river basins predicted by accumulation curves (abcissa), using the *KnowBR* package and those obtained with occurrence records (red) and after applying the proposed model approach with a Kernel density (smoothing value of 2) (blue; ordinate). Green line shows the 1:1 fit.

Fig. 3 shows the significant explanatory variables obtained from stepwise multiple regressions, considering the predicted change in species richness in the year 2070 (RCP 4.5 scenario). All the considered explanatory variables aggregated are able to explain 54% of the variance in the obtained species richness without showing a strong spatial autocorrelation (Durbin-Watson statistic 1.87, P = 0.047). The variable with the highest contribution was BIO12 (annual precipitation), so that species richness decline at higher rates in those river basins that currently have high annual precipitation values. The second variable in importance was isothermality in river basins (BIO3). Isothermality is a measure of the annual temperature range experienced on a daily basis, such that the decline was higher where current river basin temperature seasonality is high (Fig. 3).

The values of the different diversity components (richness, rarity, heterogeneity, evenness, taxonomic diversity functional diversity) were very similar between the two scenarios (Fig. 4A). The ratio of species richness in the years 2050 and 2070, as compared to the present were 0.80 and 0.78, respectively (Fig. 4). In other words, on average, in all river basins, approximately 20% of species are to be lost. Rarity was also lower in 2050
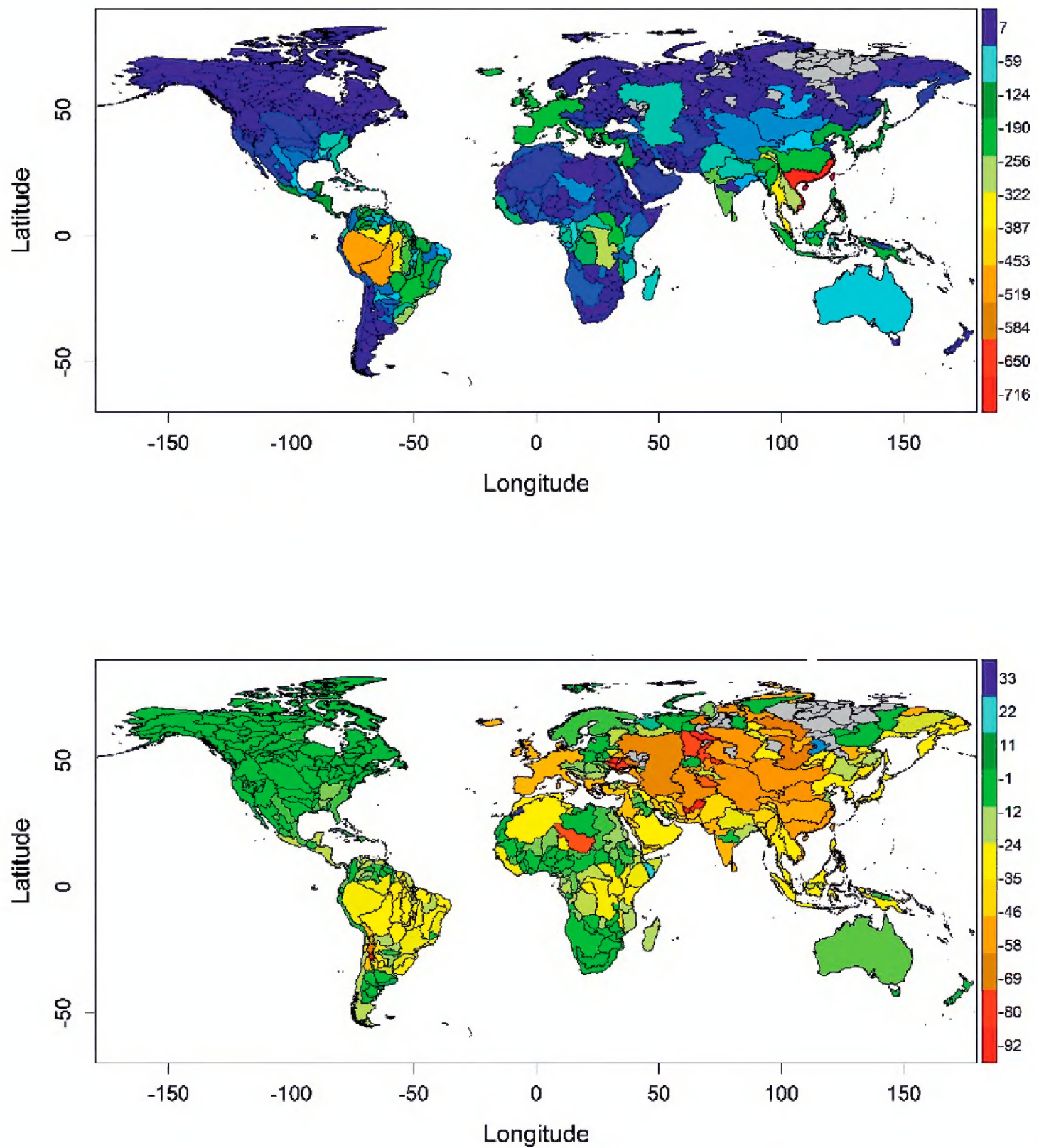
Figure 2. Predictions of the changes in species richness in river basins (in numbers in the upper panel and in percentages in the lower panel), by the year 2070 under the RCP 4.5 scenario, as compared to current species richness. The river basins with grey backgrounds had no records, no species and/or distribution model estimation was impossible. High negative values represent basins with high species extinction rates.

(mean values of 0.975 for RCP 4.5 and 0.973 for RCP 6.0) and 2070 (mean values of 0.973 for RCP 4.5 and 0.973 for RCP 6.0), as compared to the present (Fig. 4B), which means that the predicted species richness decline is partly due to the extinction of endemic or narrowly-distributed species. Heterogeneity was also lower in both years and in both scenarios, which displayed intermediate values for richness and evenness (Fig. 4C). This may be explained because heterogeneity is an index that combines the richness and
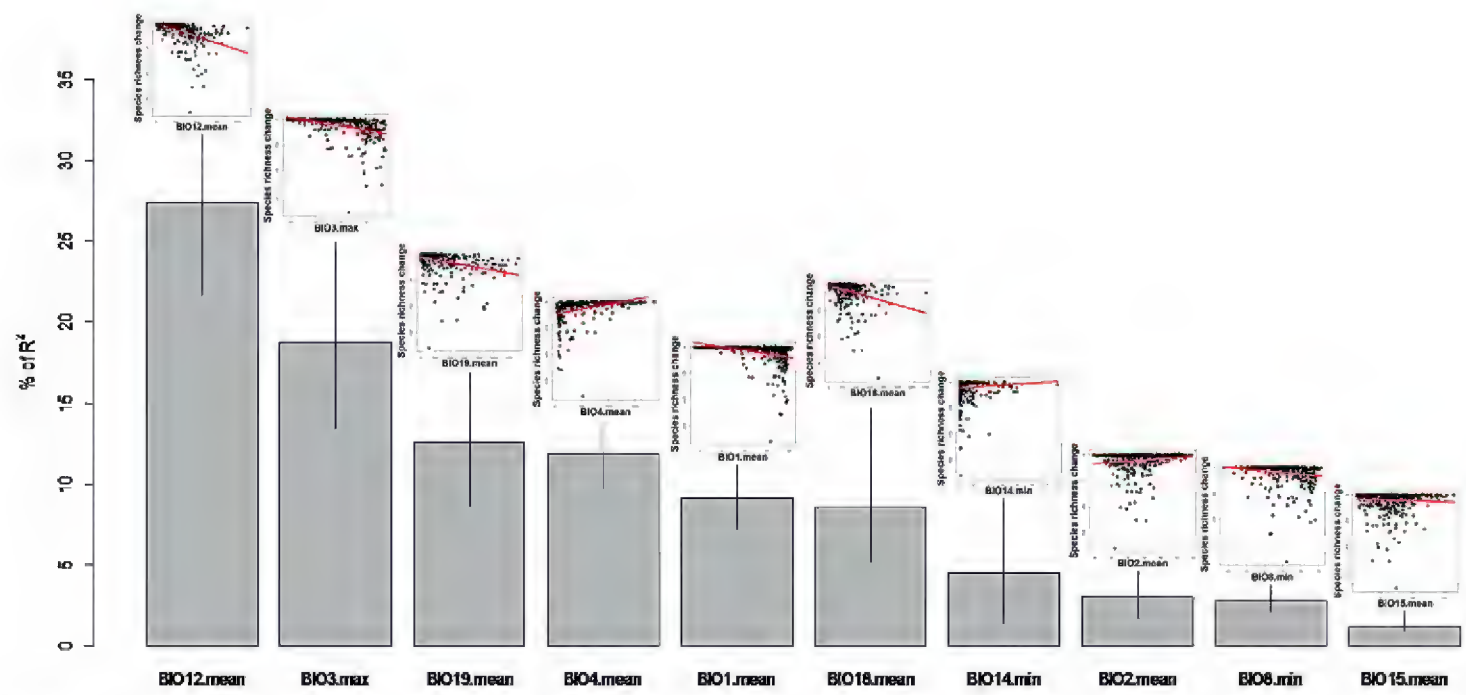
Figure 3. Relative contribution, with LMG method, of the significant climatic predictors obtained from a stepwise multiple regression, in which the dependent variable is the predicted change in species richness from the present to the year 2070 (RCP 4.5 scenario). The explanatory variables were the minimum, maximum and mean values of the climatic WorldClim variables mentioned in the Material and methods section, which were averaged for each level-two river basin. Plots above the bars show the relationships between the dependent variable and each one of the statistically-significant independent variables.
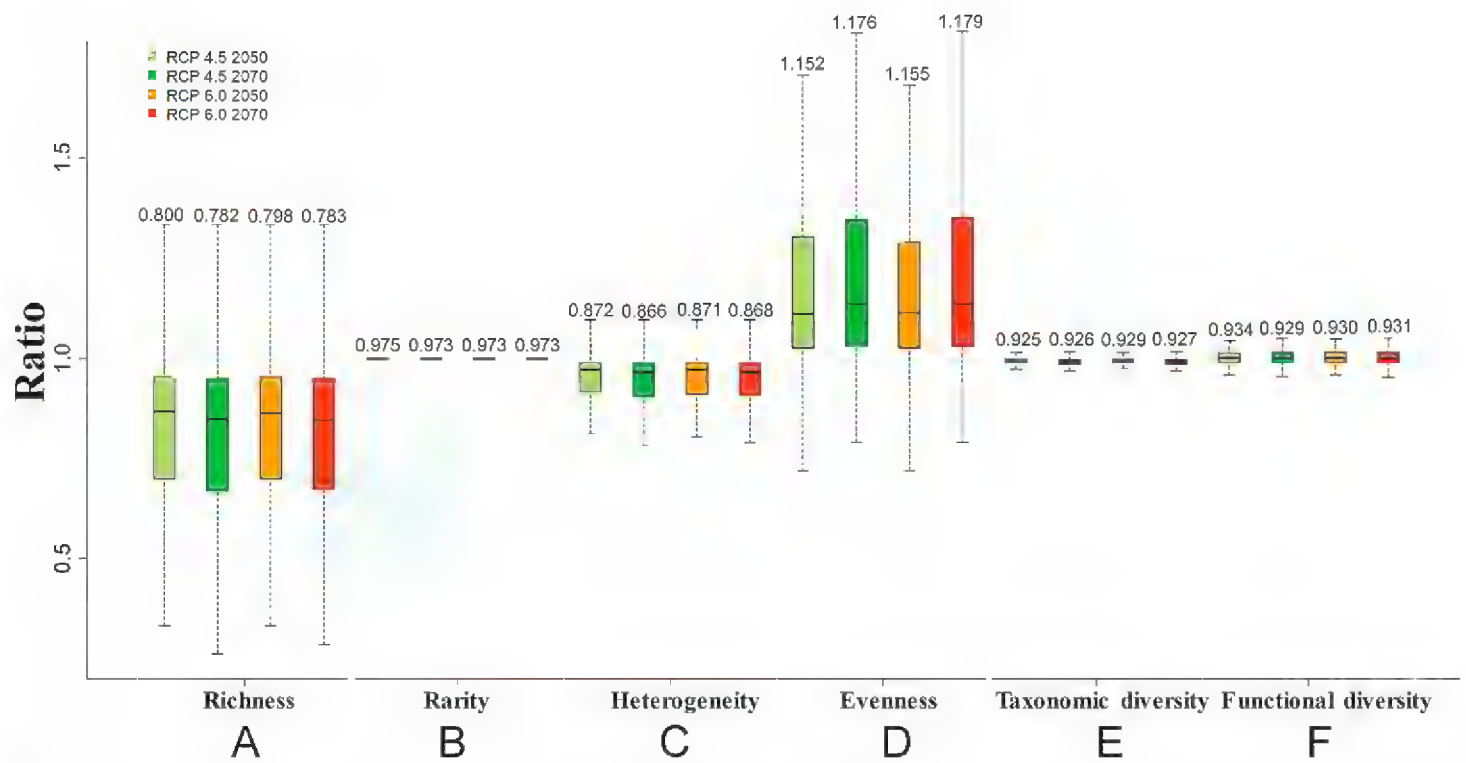
Figure 4. Boxplots of the rate of change in richness, rarity, heterogeneity (Shannon-Wiener), evenness (Simpson evenness), taxonomic diversity (taxonomic distinctness) and functional diversity (functional richness) in each river basin, as predicted for the years 2050 (RCP 4.5 scenario) and 2070 (RCP 6.0 scenario). A value less than 1 means that the Diversity Index is lower in the future scenarios than in the present and vice versa. Outliers are not shown in the boxplots. The numbers indicate median values for all river basins.
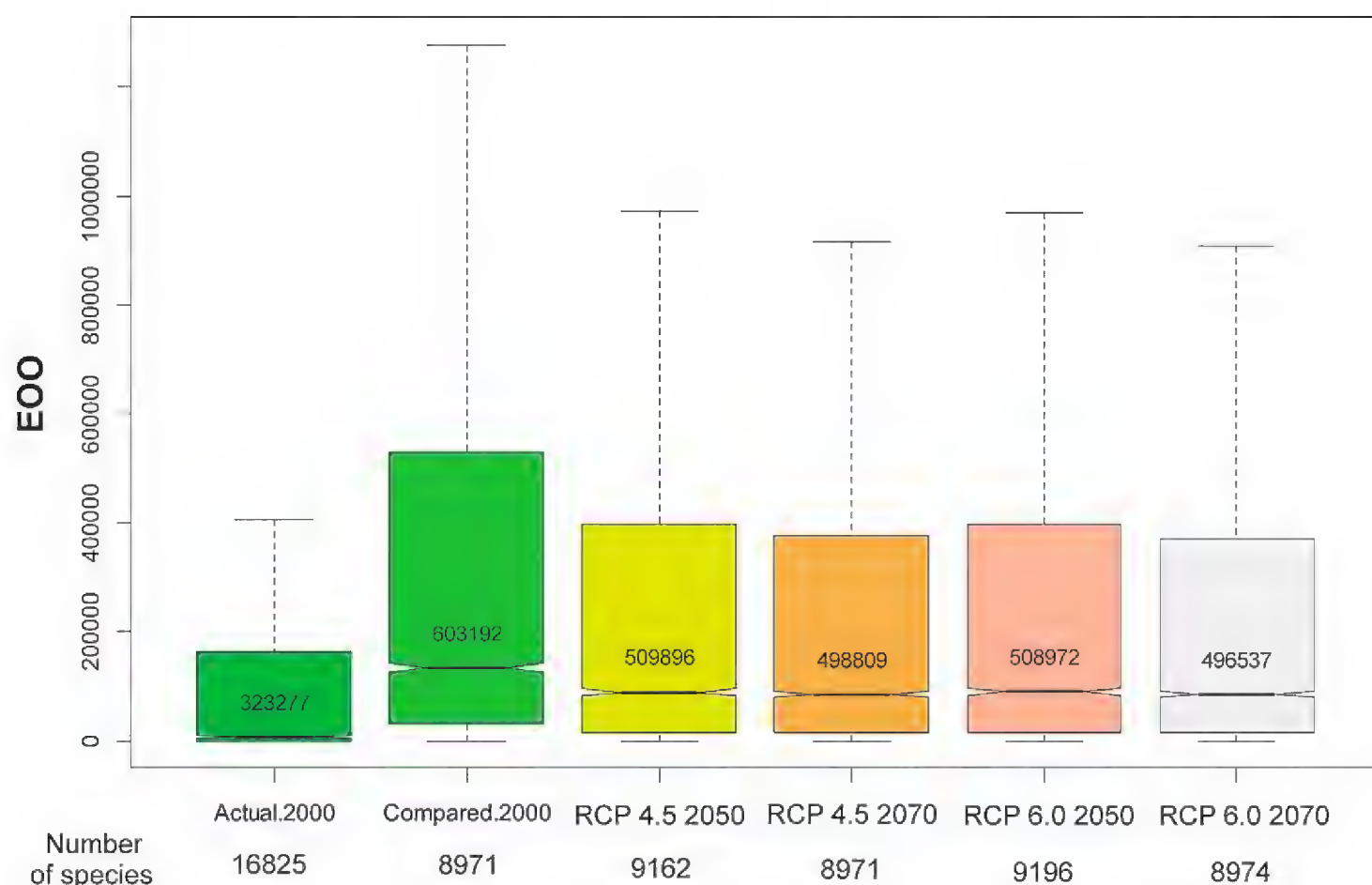
Figure 5. Boxplot showing the extent of occurrence (EOO, in km²) of the species for each scenario and year. The numbers within each plot indicate mean EOO values for all species present in each scenario. The numbers of species predicted as present in each scenario are indicated in the x-axis. The category "Compared.2000" is the mean EOO of the species in the present, but only considering those species predicted as present in the scenario with a higher number of species projected to be extinct (RCP 4.5 2070). Notched box plots show median values (horizontal line), interquartile range values between upper and lower quartiles (top and bottom of the box), distribution of 99% of data (upper and lower dashed lines) and notch lengths representing classic 95% confidence intervals. Note that, when notches do not overlap, medians may be seen to differ significantly (Krzywinski and Altman 2014) and that the difference between "Actual.2000" and "Compared.2000" scenarios is due to the predicted disappearance of species in the future.

the proportional abundance of species (Magurran 2004). Evenness, however, increased in 2050 and 2070, as compared to the present (Fig. 4D). Finally, the predicted species richness decline also led to a reduction in river basin taxonomic diversity and functional diversity (Figs 4E, F).

Fig. 5 shows further changes in the EOO estimated by the species distribution models for 2050 and 2070 in both scenarios. In addition to the above-mentioned loss of species with small geographical ranges, our results predict a general decrease in species' distributional ranges. When the median EOO of the species, for both scenarios, is compared to the median EOO from the present, it is clear that most species lose their suitable distribution area in the future (Fig. 5). These reductions in the suitable distributional area were most pronounced in the tropical areas of South America and Africa (Fig. 6), whereas at medium latitudes (approximately between 10° and 50° both North and South), the mean EOO of the remaining species in river basins was higher (Fig. 6). Interestingly, this remarkable reduction in the distribution area would be affecting mainly those species with a smaller body size (Fig. 7).
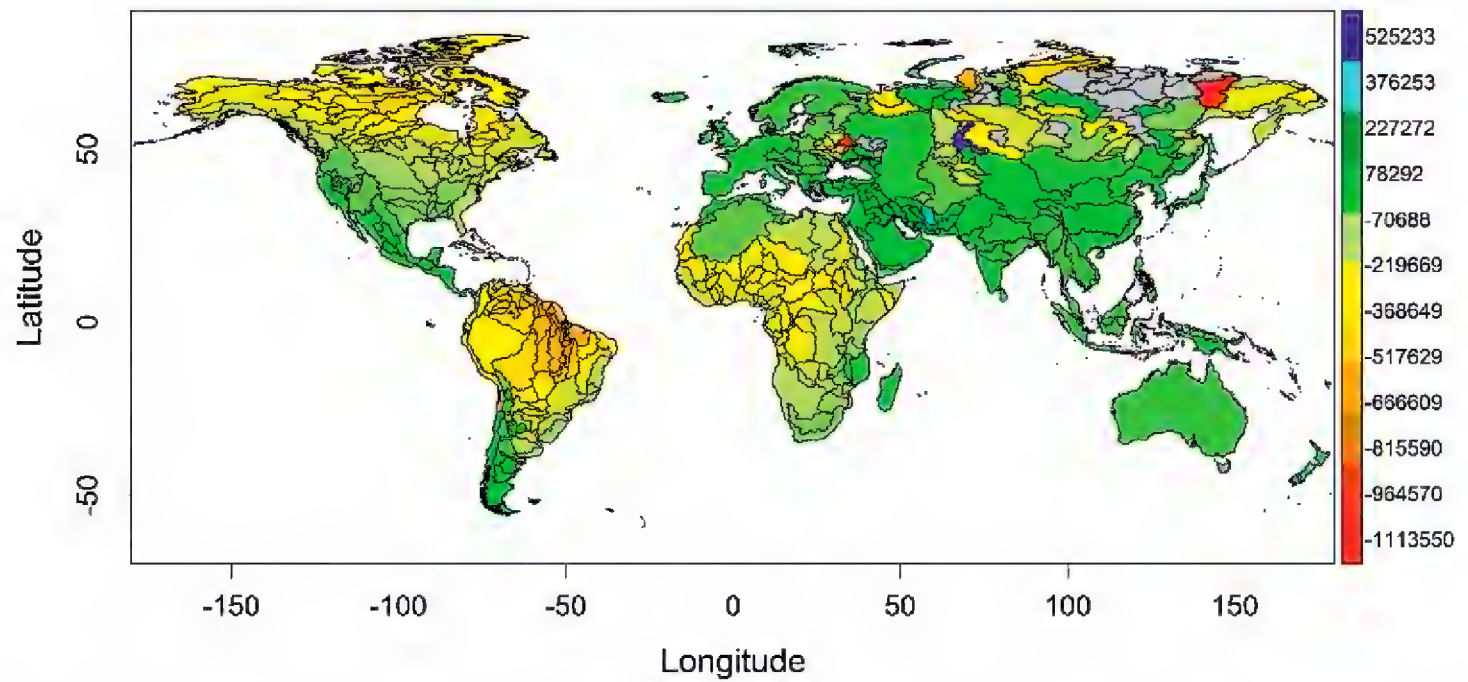
Figure 6. Predictions of the change in the Extent of Occurrence (EOO, mean value of all species present in the river basin in km²) in river basins for the year 2070, with the RCP 4.5 scenario, as compared to the current species EOO. River basins with grey backgrounds had no records, no species and/or distribution model estimation was impossible.
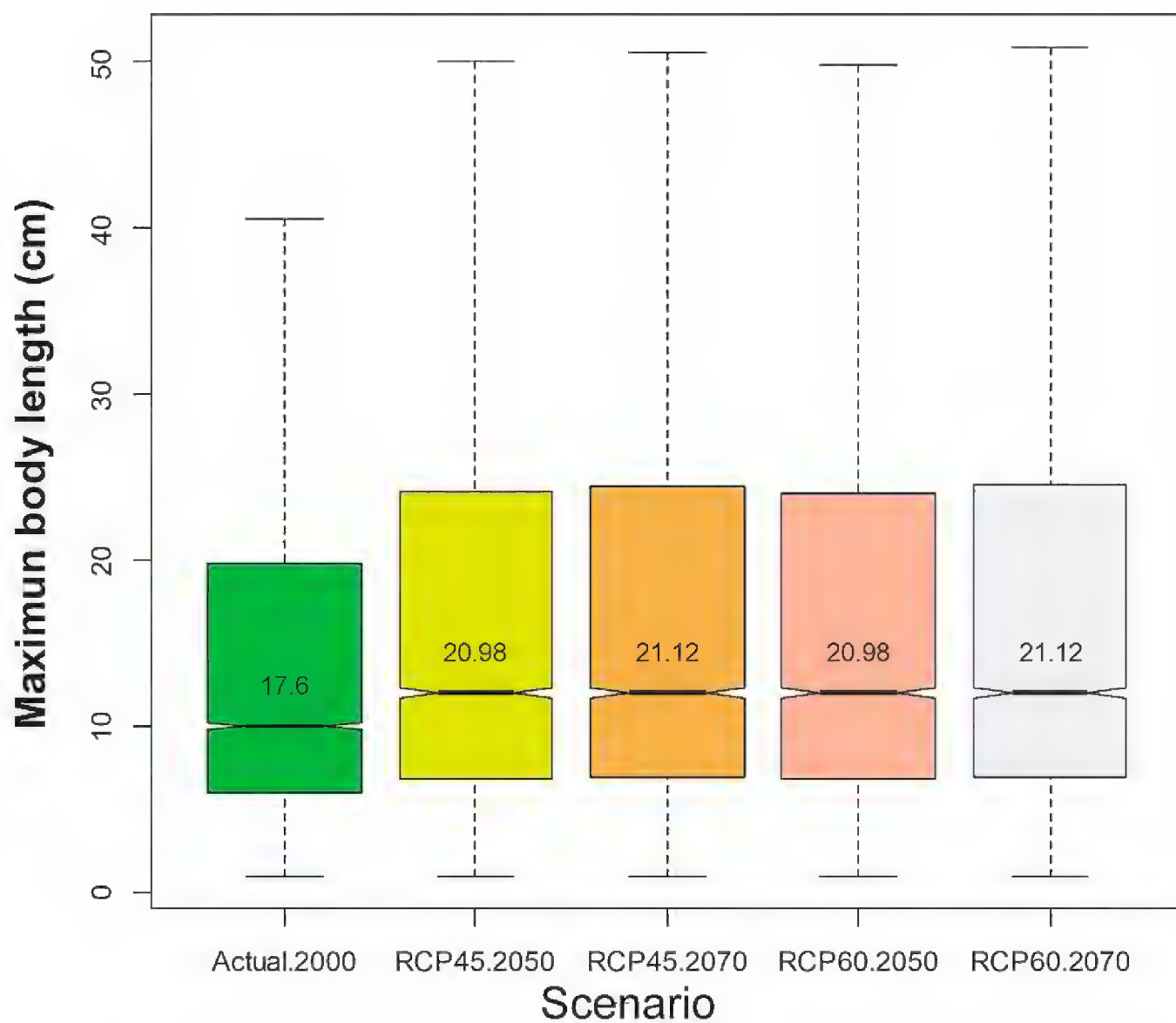
Figure 7. Boxplots with the value of the maximum body length (in cm) of species for each scenario and year. Outliers are not shown in the boxplot. The numbers indicate the mean values for all species present in each scenario.

Discussion

The comparison between the freshwater fish species richness scores, derived from accumulation curves and those generated by stacking individual SDMs, allowed the selection of the most appropriate geographical extent or accessible area (Acevedo et al. 2017), from which to derive predictions for the distribution of each species. Assuming that the congruence in the species richness estimations, provided by these two independent methods, is an indication of the accuracy of the models applied, the future geographical representations of each species were then used to estimate the potential decline and variation in the distributional area of freshwater fish. It is not possible, however, to check whether there would be changes in species composition, because the accumulation curves only provide information on species richness.

The predictions, provided by this study, are similar to those suggested by Xenopoulos et al. (2005) for freshwater fish species. However, the results obtained by Tedesco et al. (2013) contrasted greatly with the often-alarming predictions regarding climate change-driven extinction for freshwater fish (Xenopoulos et al. 2005). Furthermore, Tedesco et al. (2013) suggest that conservation action should be directed towards the current anthropogenic threats that have spurred and continue to drive, freshwater fish biodiversity loss. Although the capacity to anticipate the effects of climate change on species distributions is plagued with uncertainties (Lobo 2016), we consider that our results are consistent in suggesting the probable trajectory of freshwater fish diversity at a global scale. Future predictions are often hampered by insufficient knowledge about the effects of microclimatic variations, phenotypic plasticity, microevolution and new biological interactions, which alleviate or limit the long-term effects of the predicted climatic changes (Hoffmann and Sgro 2011; Maclean et al. 2015; Merlin et al. 2018). This would mean that the loss of diversity would be lower than shown by our correlative models. In our study, a high rate of species richness loss is predicted. We consider that this result may be partially explained by the wrong practice of extrapolating suitable areas beyond accessible river basins with current observed occurrences. Freshwater fish species are often poor dispersers (Shurin et al. 2009) and this dispersal constraint is supported by the general lack of capacity of freshwater fish species to track suitable climate conditions (Bush and Hoskins 2017; Comte and Grenouillet 2015) outside of their inhabited stream networks. This may be a consequence of river basin boundaries, which act as geographical barriers (Pelayo-Villamil et al. 2015). Thus, our previous selection of the accessible area for each species and the limitation of future predictions to these areas seem to be especially appropriate for the provision of reasonable projections. Species Distribution Models extrapolations to other time periods show, in general, that these forecasting exercises have limited capacities (Araújo et al. 2005; Maguire et al. 2016), probably as a consequence of the high number of non-climatic factors influencing species distribution and range limits (Ricklefs 2004). However, the capacity of predicting future species distribution should be higher when the ability of individuals to relocate is limited, as is the case of freshwater fish (Griffiths 2015). The vulnerability of freshwater fish communities to altered climatic patterns has been highlighted by their

isolation and fragmentation within river basins, where they act as biogeographic islands (Gozlan et al. 2010; Olden et al. 2011). In the case of freshwater fish, then, we suggest that forecasting their future spatial distribution could be facilitated by their dispersal limitations, obviating exceptions of biological invasions with human help.

The estimated predicted loss of species richness may also be attributed to the inclusion of poorly-studied tropical areas, which support elevated levels of endemism. Such endemic species may be less likely to adapt to climate change (Thieme et al. 2010). Recent findings indicate that freshwater fish species from lower latitudes and tropical warm-water habitats are at greater risk under climate change situations (Comte and Olden 2017; Payne and Smith 2017; Jarić et al. 2019). Furthermore, the results obtained suggest that the rate of extinction would be higher for species with smaller body size and/or geographical range, in agreement with previous findings (Ficke et al. 2007; Chessman 2013; Jarić et al. 2019).

These results support the species-energy theory (Hawkins et al. 2003), which predicts that cool-temperate regions experiencing warming conditions, as well as very dry regions facing increased moisture availability, are both expected to exhibit richness increases. Our models predict a higher species richness decline in those river basins with greater precipitation and also in those located in warm regions (see Figs 3, 4). The great importance of the variables related to precipitation in accounting for temporal species richness variations, in our study, differs somewhat from the results provided by other worldwide research (Buisson et al. 2008; Graham and Harrod 2009; McCullough et al. 2009), which has strongly implicated temperature warming as the major driver that will generate future changes in freshwater fish assemblages. However, our results are in agreement with those studies carried out in warmer areas (Morrongiello et al. 2011). This key difference likely reflects the primary focus of many of the accomplished studies from northern hemisphere or high-latitude freshwater environments, whereas this study was performed at the global scale.

There is an important gap, which was not considered in this study: the effect of changing flow regimes on freshwater fish diversity (Döll and Zhang 2010; Döll and Bunn 2014). The climatic variables related to precipitation (BIO12, BIO15, BIO18 and BIO19) could be considered proxies of river flow measurements (Heino et al. 2009). However, changes in seasonality or high/low flows may be not fully explained by the climatic variables applied here. One third of total fish species and one fifth of the endemic fish species in Africa occur in eco-regions that may experience a change in discharge or runoff of over 40% by the 2050s (Thieme et al. 2010). Moreover, there may also be synergies created between climatic and non-climatic anthropogenic stressors, such as deforestation, over-exploitation, habitat degradation and modification, water pollution, flow modification and hydropower generation (Döll and Zhang 2010).

In addition to the effect of climate change on species richness and geographic species range size, the climate-induced changes in taxonomic diversity observed in the present study, which have rarely been addressed for freshwater fish (Buisson and Grenouillet 2009), may result in changes in biotic interactions (competition, predation etc.) and compositional changes (Comte et al. 2013). In any case, these potential changes in

biotic interactions, which may affect species distribution, do not invalidate the use of purely climate-based model estimations for the quantification of the probable impacts of climate change on species distributions (Araújo and Luoto 2007), as shown herein. In conclusion, our results suggest a deep change in the basin assemblages of freshwater fish with the extinction of almost half of current freshwater fish species in the coming decades. This alarming prediction would particularly affect tropical regions and areas with changing water flow regimes by the greater extinction likelihood of those species with smaller body size and/or limited geographical ranges.

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References

Acevedo P, Jiménez-Valverde A, Lobo JM, Real R (2017) Predictor weighting and geographical background delimitation: Two synergetic sources of uncertainty when assessing species sensitivity to climate change. Climatic Change 145(1–2): 131–143. https://doi.org/10.1007/s10584-017-2082-1

Araújo MB, Luoto M (2007) The importance of biotic interactions for modelling species distributions under climate change. Global Ecology and Biogeography 16(6): 743–753. https://doi.org/10.1111/j.1466-8238.2007.00359.x

Araújo MB, Pearson RG, Thuiller W, Erhard M (2005) Validation of species-climate impact models under climate change. Global Change Biology 11(9): 1504–1513. https://doi.org/10.1111/j.1365-2486.2005.01000.x

Booth DJ, Bond NR, Macreadie P (2011) Detecting range shifts among Australian fishes in response to climate change. Marine & Freshwater Research 62(9): 1027–1042. https://doi.org/10.1071/MF10270

Buisson L, Grenouillet G (2009) Contrasted impacts of climate change on stream fish assemblages along an environmental gradient. Diversity & Distributions 15(4): 613–626. https://doi.org/10.1111/j.1472-4642.2009.00565.x

Buisson L, Thuiller W, Lek S, Lim P, Grenouillet G (2008) Climate change hastens the turnover of stream fish assemblages. Global Change Biology 14(10): 2232–2248. https://doi.org/10.1111/j.1365-2486.2008.01657.x

Buisson L, Grenouillet G, Villéger S, Canal J, Laffaille P (2013) Toward a loss of functional diversity in stream fish assemblages under climate change. Global Change Biology 19(2): 387–400. https://doi.org/10.1111/gcb.12056

Bush A, Hoskins AJ (2017) Does dispersal capacity matter for freshwater biodiversity under climate change? Freshwater Biology 62(2): 382–396. https://doi.org/10.1111/fwb.12874

Chessman BC (2013) Identifying species at risk from climate change: Traits predict the drought vulnerability of freshwater fishes. Biological Conservation 160: 40–49. https://doi.org/10.1016/j.biocon.2012.12.032

Clench H (1979) How to make regional lists of butterflies: Some thoughts. Journal of the Lepidopterists Society 33: 216–231.

Collen B, Whitton F, Dyer EE, Baillie JE, Cumberlidge N, Darwall WR, Pollock C, Richman NI, Soulsby A, Böhm M (2014) Global freshwater species congruence. Global Ecology and Biogeography 23: 40–51. https://doi.org/10.1111/geb.12096

Comte L, Grenouillet G (2013) Do stream fish track climate change? Assessing distribution shifts in recent decades. Ecography 36(11): 1236–1246. https://doi.org/10.1111/j.1600-0587.2013.00282.x

Comte L, Grenouillet G (2015) Distribution shifts of freshwater fish under a variable climate: Comparing climatic, bioclimatic and biotic velocities. Diversity & Distributions 21(9): 1014–1026. https://doi.org/10.1111/ddi.12346

Comte L, Olden JD (2017) Evolutionary and environmental determinants of freshwater fish thermal tolerance and plasticity. Global Change Biology 23(2): 728–736. https://doi.org/10.1111/gcb.13427

Comte L, Buisson LT, Daufresnes M, Grenouillet G (2013) Climate-induced changes in the distribution of freshwater fish: Observed and predicted trends. Freshwater Biology 58(4): 625–639. https://doi.org/10.1111/fwb.12081

Conti L, Comte L, Hugueny B, Grenouillet G (2015) Drivers of freshwater fish colonisations and extirpations under climate change. Ecography 38(5): 510–519. https://doi.org/10.1111/ecog.00753

Döll P, Bunn SE (2014) Cross-chapter box on the impact of climate change on freshwater ecosystems due to altered river flow regimes. In: Field CB, Barros VR, Dokken DJ, Mach KJ, Mastrandrea MD, Bilir TE, Chatterjee M, Ebi KL, Estrada YO, Genova RC, Girma B, Kissel ES, Levy AN, MacCracken S, Mastrandrea PR, White LL (Eds) Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, 143–146.

Döll P, Zhang J (2010) Impact of climate change on freshwater ecosystems: A global-scale analysis of ecologically relevant river flow alterations. Hydrology and Earth System Sciences 14(5): 783–799. https://doi.org/10.5194/hess-14-783-2010

Drakou EG, Bobori DC, Kallimanis AS, Mazaris AD, Sgardelis SP, Pantis JD (2009) Freshwater fish community structured more by dispersal limitation than by environmental heterogeneity. Ecology of Freshwater Fish 18: 369–379. https://doi.org/10.1111/j.1600-0633.2009.00354.x

Durbin J, Watson GS (1951) Testing for serial correlation in least squares regression. Biometrika 38(1–2): 159–171. https://doi.org/10.2307/2332325

Edwards BA, Southee FM, McDermid JL (2016) Using climate and a minimum set of local characteristics to predict the future distributions of freshwater fish in Ontario, Canada,

at the lake-scale. Global Ecology and Conservation 8: 71–84. https://doi.org/10.1016/j.gecco.2016.08.006

Eskildsen A, le Roux PC, Heikkinen RK, Høye TT, Kissling WD, Pöyry J, Wisz MS, Luoto M (2013) Testing species distribution models across space and time: High latitude butterflies and recent warming. Global Ecology and Biogeography 22(12): 1293–1303. https://doi.org/10.1111/geb.12078

Fan JY, Zhao NX, Li M, Gao WF, Wand ML, Zhu GP (2018) What are the best predictors for invasive potential of weeds? Transferability evaluations of model predictions based on diverse environmental data sets for *Flaveria bidentis*. Weed Research 58(2): 141–149. https://doi.org/10.1111/wre.12292

Ficke AD, Myrick CA, Hansen LJ (2007) Potential impacts of global climate change on freshwater fisheries. Reviews in Fish Biology and Fisheries 17(4): 581–613. https://doi.org/10.1007/s11160-007-9059-5

Filipe AF, Markovic D, Pletterbauer F, Tisseuil C, Wever A, Schmutz S, Bonada N, Freyhof J (2013) Forecasting fish distribution along stream networks: Brown trout (*Salmo trutta*) in Europe. Diversity & Distributions 19(8): 1059–1071. https://doi.org/10.1111/ddi.12086

Froese R, Pauly D (2019) FishBase. World Wide Web electronic publication. www.fishbase.org

Gallo B, Jackson MC, O'Gorman E (2017) Adaptation of freshwater species to climate change. Grantham Institute Briefing Note 8: 1–6.

García-Roselló E, Guisande C, González-Dacosta J, Heine J, Pelayo-Villamil P, Manjarrés-Hernández A, Vaamonde A, Granado-Lorencio C (2013) ModestR: A software tool for managing and analyzing species distribution map databases. Ecography 36(11): 102–1207. https://doi.org/10.1111/j.1600-0587.2013.00374.x

García-Roselló E, Guisande C, Heine J, Pelayo-Villamil P, Manjarrés-Hernández A, González-Vilas L, González-Dacosta J, Vaamonde A, Granado-Lorencio C (2014) Using ModestR to download, import and clean species distribution records. Methods in Ecology and Evolution 5(7): 703–713. https://doi.org/10.1111/2041-210X.12209

García-Roselló E, Guisande C, Manjarrés-Hernández A, González-Dacosta J, Heine J, Pelayo-Villamil P, Vari RP, Vaamonde A, Granado-Lorencio C, Lobo JM (2015) Can we derive macroecological patterns from primary GBIF data? Global Ecology and Biogeography 24: 335–347. https://doi.org/10.1111/geb.12260

García-Roselló E, Guisande C, González-Vilas L, González-Dacosta J, Heine J, Pérez-Costas E, Lobo JM (2019) A simple method to estimate the probable distribution of species. Ecography 42(9): 1613–1622. https://doi.org/10.1111/ecog.04563

González-Vilas L, Guisande C, Vari RP, Pelayo-Villamil P, Manjarrés-Hernández A, García-Roselló E, González-Dacosta J, Heine J, Pérez-Costas E, Granado-Lorencio C, Palau-Ibars A, Lobo JM (2016) Geospatial data of freshwater habitats for macroecological studies: An example with freshwater fishes. International Journal of Geographical Information Science 30(1): 126–141. https://doi.org/10.1080/13658816.2015.1072629

Gozlan RE, Britton JR, Cowx IG, Copp GH (2010) Current knowledge on non-native freshwater fish introductions. Journal of Fish Biology 76(4): 751–786. https://doi.org/10.1111/j.1095-8649.2010.02566.x

Graham CT, Harrod C (2009) Implications of climate change for the fishes of the British Isles. Journal of Fish Biology 74(6): 1143–1205. https://doi.org/10.1111/j.1095-8649.2009.02180.x

Griffiths D (2015) Connectivity and vagility determine spatial richness gradients and diversification of freshwater fish in North America and Europe. Biological Journal of the Linnean Society. Linnean Society of London 116(4): 773–786. https://doi.org/10.1111/bij.12638

Grömping U (2006) Relative Importance for Linear Regression in R: The Package relaimpo. Journal of Statistical Software 17(1): 1–27. https://doi.org/10.18637/jss.v017.i01

Grömping U (2018) Relative Importance of Regressors in Linear Models. R package version 2.2-3. https://cran.r-project.org/web/packages/relaimpo [Accessed 20 September 2018]

Guisande C (2018a) Ecological Indicators. R package version 1.4. https://cran.r-project.org/web/packages/EcoIndR [Accessed 25 November 2018]

Guisande C (2018b) Estimation of the relative importance of factors affecting species distribution based on stability concept. R package version 1.6. https://cran.r-project.org/web/packages/SPEDInstabR [Accessed 6 February 2018]

Guisande C, Lobo JM (2018) Discriminating well surveyed spatial units from exhaustive biodiversity databases. R package version 1.3. https://cran.r-project.org/web/packages/KnowBR [Accessed 5 July 2018]

Guisande C, Manjarrés-Hernández A, Pelayo-Villamil P, Granado-Lorencio C, Riveiro I, Acuña A, Prieto-Piraquive E, Janeiro E, Matías JM, Patti C, Patti B, Mazzola S, Jiménez S, Duque V, Salmerón F (2010) IPez: An expert system for the taxonomic identification of fishes based on machine learning techniques. Fisheries Research 102(3): 240–247. https://doi.org/10.1016/j.fishres.2009.12.003

Guisande C, Barreiro A, Vaamonde A (2011) Tratamiento de datos con R, Statistica y SPSS. Ediciones Díaz de Santos, Madrid.

Guisande C, Heine J, González-DaCosta J, García-Roselló E (2014) RWizard Software. University of Vigo, Vigo, Spain. Diversity 7(4): 385–396. https://doi.org/10.3390/d7040385

Guisande C, García-Roselló E, Heine J, González-Dacosta J, Gozález-Vilas L, García Pérez BJ, Lobo JM (2017a) SPEDInstabR: An algorithm based on a fluctuation index for selecting predictors in species distribution modeling. Ecological Informatics 37: 18–23. https://doi.org/10.1016/j.ecoinf.2016.11.004

Guisande C, Heine J, García-Roselló E, González-Dacosta J, González-Vilas L, García Pérez BJ (2017b) DER: An algorithm for comparing species diversity between assemblages. Ecological Indicators 81: 41–46. https://doi.org/10.1016/j.ecolind.2017.05.049

Hauer FR, Baron JS, Campbell DH, Fausch KD, Hostetler SW, Leavesley GH, Leavitt PR, Mcknight DM, Stanford JA (1997) Assessment of climate change and freshwater ecosystems of the Rocky Mountains, USA and Canada. Hydrological Processes 11(8): 903–924. https://doi.org/10.1002/(SICI)1099-1085(19970630)11:8%3C903::AID-HYP511%3E3.0.CO;2-7

Hawkins BA, Howard RF, Cornell V, Currie DJ, Guégan JF, Kaufman DM, Kerr JT, Mittelbach GG, Oberdorff T, O'Brien EM, Porter EE, Turner JRG (2003) Energy, water, and broad-scale geographic patterns of species richness. Ecology 84(12): 3105–3117. https://doi.org/10.1890/03-8006

Heino J, Virkalla R, Toivonen H (2009) Climate change and freshwater biodiversity: Detected patterns, future trends and adaptations in northern regions. Biological Reviews of the Cambridge Philosophical Society 84(1): 39–54. https://doi.org/10.1111/j.1469-185X.2008.00060.x

Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology 25(15): 1965–1978. https://doi.org/10.1002/joc.1276

Hoffmann AA, Sgro CM (2011) Climate change and evolutionary adaptation. Nature 470(7335): 479–485. https://doi.org/10.1038/nature09670

Hortal J, Lobo JM (2005) An ED-based protocol for the optimal sampling of biodiversity. Biodiversity and Conservation 14(12): 2913–2947. https://doi.org/10.1007/s10531-004-0224-z

Hothorn T, Zeileis A, Farebrother RW, Cummins C, Millo G, Mitchell D (2018) Testing Linear Regression Models. R package version 0.9-36. R package version 1.4. https://cran.r-project.org/web/packages/lmtest [Accessed 5 September 2018]

Jarić I, Lennox RJ, Kalinkat G, Cvijanović G, Radinger J (2019) Susceptibility of European freshwater fish to climate change: Species profiling based on life-history and environmental characteristics. Global Change Biology 25(2): 448–458. https://doi.org/10.1111/gcb.14518

Kharouba HM, Algar AC, Kerr JT (2009) Historically calibrated predictions of butterfly species' range shift using global change as a pseudo-experiment. Ecology 90(8): 2213–2222. https://doi.org/10.1890/08-1304.1

Ko CY, Ko CJ, Lin RS, Lee PF (2013) Influences of temporal independence of data on modelling species distributions. Basic and Applied Ecology 14(4): 309–319. https://doi.org/10.1016/j.baae.2013.04.003

Krzywinski M, Altman N (2014) Visualizing samples with box plots. Nature Methods 11(2): 119–120. https://doi.org/10.1038/nmeth.2813

Lobo JM (2016) The use of occurrence data to predict the effects of climate change on insects. Current Opinion in Insect Science 17: 62–68. https://doi.org/10.1016/j.cois.2016.07.003

Lobo JM, Hortal J, Yela JL, Millán A, Sánchez-Fernández D, García-Roselló E, González-Dacosta J, Heine J, González-Vilas L, Guisande C (2018) KnowBR: An application to map the geographical variation of survey effort and identify well-surveyed areas from biodiversity databases. Ecological Indicators 91: 241–248. https://doi.org/10.1016/j.ecolind.2018.03.077

Maclean IMD, Hopkins JJ, Bennie J, Lawson CR, Wilson RJ (2015) Microclimates buffer the responses of plant communities to climate change. Global Ecology and Biogeography 24(11): 1340–1350. https://doi.org/10.1111/geb.12359

Maguire KC, Nieto-Lugilde D, Blois JL, Fitzpatrick MC, Williams JW, Ferrier S, Lorenz DJ (2016) Controlled comparison of species- and community-level models across novel climates and communities. Proceedings of the Royal Society B – Biological Sciences 283(1826): 20152817. https://doi.org/10.1098/rspb.2015.2817

Magurran AE (2004) Measuring biological diversity. Blackwell, Oxford.

Manjarrés-Hernández AM, Guisande C, García-Roselló E, Pelayo-Villamil P, González-Dacosta J, Heine J, González-Vilas L, Granado-Lorencio C, Duque SR, Lobo JM (2018) A

procedure to assess the spatial variability in the importance of abiotic factors affecting distributions: The case of world freshwater fishes. Current Zoology 64(5): 549–557. https://doi.org/10.1093/cz/zox063

Markovic D, Freyhof J, Wolter C (2012) Where are all the fish: Potential of biogeographical maps to project current and future distribution patterns of freshwater species. PLoS ONE 7: e40530. https://doi.org/10.1371/journal.pone.0040530

Markovic D, Carrizo SF, Kärcher O, Walz A, David JN (2017) Vulnerability of European freshwater catchments to climate change. Global Change Biology 23: 3567–3580. https://doi.org/10.1111/gcb.13657

McCullough DA, Bartholow JM, Jager HI, Beschta RL, Cheslak EF, Deas ML, Ebersole JL, Foott JS, Johnson SL, Marine KR, Mesa MG, Petersen JH, Souchon Y, Tiffan KF, Wurtsbaugh WA (2009) Research in thermal biology: Burning questions for coldwater stream fishes. Reviews in Fisheries Science 17(1): 90–115. https://doi.org/10.1080/10641260802590152

Merlin M, Duputie A, Chuine I (2018) Limited validation of forecasted northward range shift in ten European tree species from a common garden experiment. Forest Ecology and Management 410: 144–156. https://doi.org/10.1016/j.foreco.2018.01.001

Morrongiello JR, Beatty SJ, Bennett JC, Crook DA, Ikedife DNEN, Kennard MJ, Kerezsy A, Lintermans M, McNeil DG, Pusey BJ, Rayner T (2011) Climate change and its implications for Australia's freshwater fish. Marine & Freshwater Research 62(9): 1082–1098. https://doi.org/10.1071/MF10308

Olden JD, Kennard MJ, Lawler JJ, Poff NL (2011) Challenges and opportunities in implementing managed relocation for conservation of freshwater species. Conservation Biology 25: 40–47. https://doi.org/10.1111/j.1523-1739.2010.01557.x

Payne NL, Smith JA (2017) An alternative explanation for global trends in thermal tolerance. Ecology Letters 20(1): 70–77. https://doi.org/10.1111/ele.12707

Pearson RG, Dawson TP (2003) Predicting the impacts of climate change on the distribution of species: Are bioclimate envelope models useful? Global Ecology and Biogeography 12(5): 361–371. https://doi.org/10.1046/j.1466-822X.2003.00042.x

Pelayo-Villamil P, Guisande C, González-Vilas L, Carvajal-Quintero JD, Jiménez-Segura LF, García-Roselló E, Heine J, González-Dacosta J, Manjarrés-Hernández A, Vaamonde A, Granado-Lorencio A (2012) ModestR: Una herramienta informática para el estudio de los ecosistemas acuáticos de Colombia. Actualidades Biologicas 34: 225–239.

Pelayo-Villamil P, Guisande C, Vari RP, Manjarrés-Hernández A, García-Roselló E, González-Dacosta J, Heine J, González-Vilas L, Patti B, Quinci EM, Jiménez LF, Granado-Lorencio C, Tedesco PA, Lobo JM (2015) Global diversity patterns of freshwater fishes-Potential victims of their own success. Diversity & Distributions 21(3): 345–356. https://doi.org/10.1111/ddi.12271

Pelayo-Villamil P, Guisande C, Manjarrés-Hernández A, Jiménez LF, Granado-Lorencio C, García-Roselló E, González-Dacosta J, Heine J, González-Vilas L, Lobo JM (2018) Completeness of national freshwater fish species inventories around the world. Biodiversity and Conservation 27(14): 3807–3817. https://doi.org/10.1007/s10531-018-1630-y

Pérez-Costas E, Guisande C, González-Vilas L, García-Roselló E, Heine J, González-Dacosta J, Lobo JM (2019) NOO3D: A procedure to perform 3D species distribution models. Ecological Informatics 54: 101008. https://doi.org/10.1016/j.ecoinf.2019.101008

Pfafstetter O (1989) Classification of hydrographic basins: coding methodology. Unpublished manuscript, Departamento Nacional de Obras de Saneamento, August 18, 1989, Rio de Janeiro available from J.P. Verdin, U.S. Geological Survey, EROS Data Center, Sioux Falls, South Dakota 57198 USA.

R Development Core Team (2018) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Radinger J, Essl F, Hölker F, Horký P, Slavík O, Wolter C (2017) The future distribution of river fish: The complex interplay of climate and land use changes, species dispersal and movement barriers. Global Change Biology 23(11): 4970–4986. https://doi.org/10.1111/gcb.13760

Rapacciuolo G, Roy DB, Gillings S, Fox R, Walker K, Purvis A (2012) Climatic associations of British species distributions show good transferability in time but low predictive accuracy for range change. PLoS ONE 7(7): e40212. https://doi.org/10.1371/journal.pone.0040212

Ricklefs RE (2004) A comprehensive framework for global patterns in biodiversity. Ecology Letters 7(1): 1–15. https://doi.org/10.1046/j.1461-0248.2003.00554.x

Rubidge EM, Monahan WB, Parra JL, Cameron SE, Brashares JS (2011) The role of climate, habitat, and species co-occurrence as drivers of change in small mammal distributions over the past century. Global Change Biology 17(2): 696–708. https://doi.org/10.1111/j.1365-2486.2010.02297.x

Ruiz-Navarro A, Gillingham PK, Britton JR (2016) Predicting shifts in the climate space of freshwater fishes in Great Britain due to climate change. Biological Conservation 203: 33–42. https://doi.org/10.1016/j.biocon.2016.08.021

Shurin JB, Cottenie K, Hillebrand H (2009) Spatial autocorrelation and dispersal limitation in freshwater organisms. Oecologia 159(1): 151–159. https://doi.org/10.1007/s00442-008-1174-z

Soberón J, Llorente BJ (1993) The use of species accumulation functions for the prediction of species richness. Conservation Biology 7(3): 480–488. https://doi.org/10.1046/j.1523-1739.1993.07030480.x

Tedesco PA, Oberdorff T, Cornu JF, Beauchard O, Brosse S, Dürr HH, Grenouillet G, Leprieur F, Tisseuil C, Zaiss R, Hugueny B (2013) A scenario for impacts of water availability loss due to climate change on riverine fish extinction rates. Journal of Applied Ecology 50: 1105–1115. https://doi.org/10.1111/1365-2664.12125

Thieme ML, Lehner B, Abell R, Matthews J (2010) Exposure of Africa's freshwater biodiversity to a changing climate. Conservation Letters 3: 324–331. https://doi.org/10.1111/j.1755-263X.2010.00120.x

Verdin KL, Greenlee SK (1998) HYDRO1k Documentation. US Geological Survey [online]. http://webgis.wr.usgs.gov/globalgis/metadata_qr/metadata/hydro1k.htm [accessed 18 February 2016]

Warren R, Price J, Graham E, Forstenhaeusler N, VanDerWal J (2018) The projected effect on insects, vertebrates, and plants of limiting global warming to 1.5 °C rather than 2 °C. Science 360(6390): 791–795. https://doi.org/10.1126/science.aar3646

Watling JI, Bucklin DN, Speroterra C, Brandt LA, Mazzotti FJ, Romañach SS (2013) Validating predictions from climate envelope models. PLoS ONE 8(5): e63600. https://doi.org/10.1371/journal.pone.0063600

Xenopoulos MA, Lodge DM, Alcamo J, Märker M, Schulze K, Van Vuuren DP (2005) Scenarios of freshwater fish extinctions from climate change and water withdrawal. Global Change Biology 11(10): 1557–1564. https://doi.org/10.1111/j.1365-2486.2005.001008.x

Supplementary material 1

Appendix 1

Authors: Ana Manjarrés-Hernández, Cástor Guisande, Emilio García-Roselló, Juergen Heine, Patricia Pelayo-Villamil, Elisa Pérez-Costas, Luis González-Vilas, Jacinto González-Dacosta, Santiago R. Duque, Carlos Granado-Lorencio, Jorge M. Lobo

Data type: data occurrences

Explanation note: Sources describing all the data downloaded from the Global Biodiversity Information Facility (GBIF; see https://www.gbif.org/), which were used in this study.

Link: https://doi.org/10.3897/natureconservation.43.58997.suppl1

Supplementary material 2

Table S1

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Data type: species data

Explanation note: Description of the species included in the analysis, as well as future species predictions in 2050 and 2070 and under both scenarios. If a species is categorised as "NOT", the complete disappearance of their distributional area is predicted. The maximum body length of each species is also included, obtained from https://www.fishbase.org/ or from the original manuscripts, when not available at FishBase.

Link: https://doi.org/10.3897/natureconservation.43.58997.suppl2

Supplementary material 3

Appendix 2

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Data type: species data

Explanation note: Biological traits assigned to each one of the considered species. We used 6 traits divided into three biological functions: food acquisition, life habitat and locomotion. Food acquisition traits include the feeding habitat (pelagic, benthopelagic and benthic) and the trophic guild (primary consumer, secondary consumer, top-predator, omnivorous and detritivorous). Life habitat traits comprise habitat type (pelagic, benthopelagic and demersal) and migration type (potamodromous, anadromous, catadromous, amphidromous, oceanodromous and no migration). Finally, locomotion traits include body length (in cm: small < 15, medium 15–50, large 50–150 and extra-large > 150) and rheophily (rheophilic, limnophilic and eurytopic).

Link: https://doi.org/10.3897/natureconservation.43.58997.suppl3

Supplementary material 4

Appendix 3

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Data type: tutorial

Explanation note: Full description of the NOO3D procedure followed to predict the future distribution of world freshwater fish.

Link: https://doi.org/10.3897/natureconservation.43.58997.suppl4